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The impact of mountain pine beetle outbreaks and their treatment methods on the abundance of plant-foods important to caribou and grizzly bears

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ABSTRACT

In Alberta, Canada, mountain pine beetle (MPB) infestations overlap with threatened caribou and grizzly bear ranges. While MPB is a natural part of the ecosystem, increased intensity of infestation due to fire suppression and a changing climate has required mitigating actions in the form of MPB control treatments, including accelerated forest harvesting, prescribed burns, and single-tree cut and burn. However, little is known on how MPB and MPB treatments affect understory shrub and forb forage taxa important to threatened caribou and grizzly bear populations. Using data collected in west-central and north-west Alberta, we investigated how the occurrence and abundance of 25 shrub and forb taxa varied among MPB kill, MPB treatments: single-tree cut and burn, harvesting, fire, and uncut forest strata. We determined that MPB kill and MPB treatments impacted 13 forage taxa preferred by threatened caribou and grizzly bear populations. These caribou and grizzly bear forage taxa generally had a positive response to MPB kill and single-tree cut and burn, a positive response to fire, or a positive response to MPB kill, single-tree cut and burn, and fire. Our results suggest that less-intensive MPB treatments like single-tree cut and burn might balance the threat of MPB against maintaining food resources and habitat for threatened species. As MPB continues to be a significant problem in Alberta and across the boreal forest, the results from our study, combined with ongoing assessments on the impact of MPB on wildlife species will provide essential information for evidence-based landscape management.

1. Introduction

Pest and pathogen outbreaks affect ecosystem function and can have severe ecological and economic impacts (Logan et al., 2003). When pest and pathogen outbreaks have the potential to impact resource extraction activities such as forestry or fisheries, mitigating the impacts of outbreaks generally involves aggressive eradication (Dunn & Hatcher, 2015; Logan et al., 2003). However, eradication programs can have unintended effects on non-target species, including species of conservation concern (Lampert et al., 2014; Nobert et al., 2020; Norton, 2009). Effective landscape management balances multiple threats like pest and pathogen outbreaks and habitat disturbance, as well as the needs of multiple species and ecosystem processes (Carwardine et al., 2019; Lundquist et al., 2002). Nevertheless, effective landscape management is challenging to achieve due to limited resources (Martin et al., 2012), potential impacts on industrial revenues and human needs, the high cost of implementing recovery efforts (Hebblewhite, 2017), and often, a lack of information on how ecosystems respond to threats and the management actions taken to address these threats (Canessa et al., 2015).

In western Canada, mountain pine beetle (*Dendroctonus ponderosae*, hereafter MPB) is a natural part of pine forest ecosystems (Dhar et al., 2016). Although MPB outbreaks have been observed since the early 1900s, more recently the geographic extent of infestations has dramatically increased due to fire suppression increasing the availability of mature trees preferred by female MPB for egg laying (Dhar et al., 2016; Taylor & Carroll, 2004), and climate-change-driven milder winters increasing overwinter survival of larvae (Fauria & Johnson, 2009; Sambaraju et al., 2012; Stahl et al., 2006). Over the past two decades, there has been a surge of MPB in western Canada, extending across British Columbia into Alberta (Bleiker et al., 2019). MPB has the potential to infest multiple pine species including lodgepole pine (*Pinus contorta*), jack pine (*Pinus banksiana*), limber pine (*Pinus flexilis*), and white bark pine (*Pinus albicaulis*) (Cooke & Carroll, 2017; Cullingham et al., 2011; Logan et al., 2010). MPB can rapidly kill forests at

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landscape-scales as MPB burying through bark disrupts water and nutrient supply to trees, leading to tree death often within a year (Dhar et al., 2016; Safranyik & Carroll, 2006).

To contend with MPB, forestry is implementing management in areas with active infestations, including accelerated harvest of pine, single-tree cut and burn (where individual infested trees are cut down and burned leaving surrounding healthy forest intact), and prescribed burns (Amoroso et al., 2013; Alberta Sustainable Resources Development, 2007). MPB infestation and MPB treatments affect understory plants and important forage for wildlife by altering forest structure and environmental conditions, increasing light penetration and precipitation to the forest floor (Lampert et al., 2014; Nobert et al., 2020; Pec et al., 2015; Saab et al., 2014). However, there is a lack of taxa-specific knowledge on the impacts of MPB infestations and MPB treatments on understory vegetation, including impacts on taxa important as wildlife forage. Understanding these impacts is important to inform effective management plans that aim to mitigate the impact of MPB and sustain important plant-food resources, including plant-food resources preferred by threatened wildlife species.

In Alberta, woodland caribou (*Rangifer tarandus,* hereafter caribou) and grizzly bears (*Ursus arctos*) are threatened species (Alberta Grizzly Bear Recovery Team, 2008; Environment Canada, 2012). For both species, a large amount of their spring, summer, and fall diets consists of vascular plants, specifically shrubs and forbs (Denryter et al., 2017; Munro et al., 2006). Caribou and grizzly bear ranges overlap with the current MPB infestation, so MPB infestations and treatments have the potential to affect the distribution and abundance of important food resources for these threatened species. Caribou rely on mature pine forest for terrestrial and arboreal lichen forage during winter (Johnson et al., 2000; Thomas et al., 1996b; Thompson et al., 2014), and as a refuge from predators (Courbin et al., 2009); generally avoiding early seral habitat created by anthropogenic activity and wildfires (DeCesare et al., 2012; Johnson et al., 2015; Rudolph et al., 2019). Therefore, MPB treatments can conflict with caribou conservation initiatives to maintain mature forests, including pine forests, across landscapes (Environment Canada, 2012; Alberta Sustainable Resources Development, 2007). For grizzly bears who forage in open habitats, including early seral forests, forest edges, and forestry harvest blocks (Colton et al., 2021; Larsen et al., 2019; Souliere et al., 2020), MPB and MPB treatments may have positive impacts on the grizzly bear population by increasing the abundance of important understory food resources.

Shrubs and forbs become available for consumption during spring green-up and, although there is variation among species in terms of phenology and nutrition, generally these plants are available from spring into fall (McClelland et al., 2020; Munro et al., 2006). Although caribou diets are dominated by terrestrial and arboreal lichens, outside of winter their diet shifts towards deciduous shrubs, grasses, sedges, and forbs (Barten et al., 2001; Bergerud, 1972; Denryter et al., 2017; Thomas et al., 1996a; Thompson et al., 2014). For grizzly bears, while animal matter, insects, and roots are a large part of their diet, and are consumed throughout the active period, forbs make up the majority of their diet from late spring into summer (Munro et al., 2006). During fall, grizzly bear diet shifts to fruit-bearing shrubs, which are consumed in large quantities to build up enough fat reserves for hibernation (Coogan et al., 2014; Pigeon et al., 2016). There is currently a lack of information on how the shrubs and forbs that make up large portions of the diet of these two threatened species might be affected by MPB infestations and treatments.

In this study our goal was to determine the effects of MPB and MPB treatments on the distribution and abundance of 25 shrub and forb taxa important in caribou and grizzly bear diets by combining field observations and remotely sensed environmental variables. We collected field data across five strata representing MPB infestations and MPB treatment approaches: MPB kill (forest that has been infested by MPB), MPB control (forest that had single-tree cut and burn control); fire (forest that has burned due to wildfires, a proxy for prescribed burns which were rare in our study area), cut (forest that has been clear-cut harvested), and uncut (old growth fire origin stands > 50 years old). We define MPB kill and MPB control as less intensive treatments, and stand replacing treatments, cut and fire, as more intensive treatments. We hypothesized that MPB and MPB treatments would affect the abundance and distribution of shrubs and forbs. Specifically, we predicted that i) more intensive treatments would positively influence grizzly bears foods, which are generally disturbance-tolerant and/or shade-intolerant taxa (Colton et al., 2021), ii) as caribou foods include shade-intolerant and pioneer taxa (e.g., willows, alders, birches, and grasses; (Humbert et al., 2007; Hynynen et al., 2010; Urlia et al., 2020), caribou foods would have a positive response to intensive and less intensive treatments, and iii) by thinning canopies and reducing competition, less intensive treatments would also positively influence several shade-tolerant species (e.g., sedges, twisted stalk; Humbert et al., 2007). Results of this study will provide information fundamental to efficiently manage MPB impacts across the pine-dominant boreal forest of Canada, while simultaneously considering the effects of MPB infestations and treatments on forage important for threatened wildlife.

2. Methods

2.1. Study area

Our study areas were caribou ranges in west-central and north-west Alberta, Canada (Fig. 1). The west-central study area included the ranges of the À la Pêche, Narraway, and Redrock-Prairie Creek central mountain populations (COSEWIC, 2011), the boreal Little Smoky population, and portions of the Grand Cache bear management area (Alberta Environment and Parks, 2020). The north-west study area included the range of the Chinchaga boreal caribou population (COSEWIC, 2011) and portions of the Alberta North bear management area. Combined, the study areas were 33,000 km^2. The majority of each study area is provincially managed public lands where resource extraction, including mining, oil and gas and forestry, and recreation, including off road vehicle use, hiking, hunting, and fishing occur.

Forests in the uplands are dominated by lodgepole pine, white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*), and trembling aspen (*Populus tremuloides*), while in low lying wet areas, black spruce (*Picea mariana*) and tamarack (*Larix laricina*) are prominent. In the west-central study area, Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) occur at higher elevations of the Rocky Mountains. Dominant shrubs and forbs in both regions include, willow (*Salix spp*.), bog birch (*Betula pumila*), green alder (*Alnus crispa*), wild rose (*Rosa acicularis*), clovers (*Trifolium* spp.*),* dandelion (*Taraxacum officinale*), and fireweeds (*Chamerion spp*.). Ungulates in both study areas include moose (*Alces alces*), elk (*Cervus Canadensis*), mule deer and, white-tailed deer (*Odocoileus hemonius* and *Odocoileus virginianus*, respectively). The high-elevation portion of the west-central study area also has bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*). Large predators in the region include black bears (*Ursus americanus*), cougars (*Puma concolor*), wolves (*Canis lupus*), coyotes (*Canis latrans*), lynx (*Lynx Canadensis*), and wolverines (*Gulo gulo*).

2.2. Field data collection and field variables

We collected data from 774 transects across the study areas (565 in west-central and 209 in the north-west) during the summers of 2014 and 2015. Transects were 25 m in length with subplots located at 5 m intervals along each transect and were located a minimum of 300 m from other transects within the same strata. Transects were randomly selected within each of the five strata using a random number generator: MPB kill (176 transects), MPB control (133 transects), fire (85 transects), cut (258 transects), and uncut (122 transects). To select cut and uncut sites we used forest inventory data from local forestry companies. To select MPB kill, MPB control and, fire sites we used data obtained from the

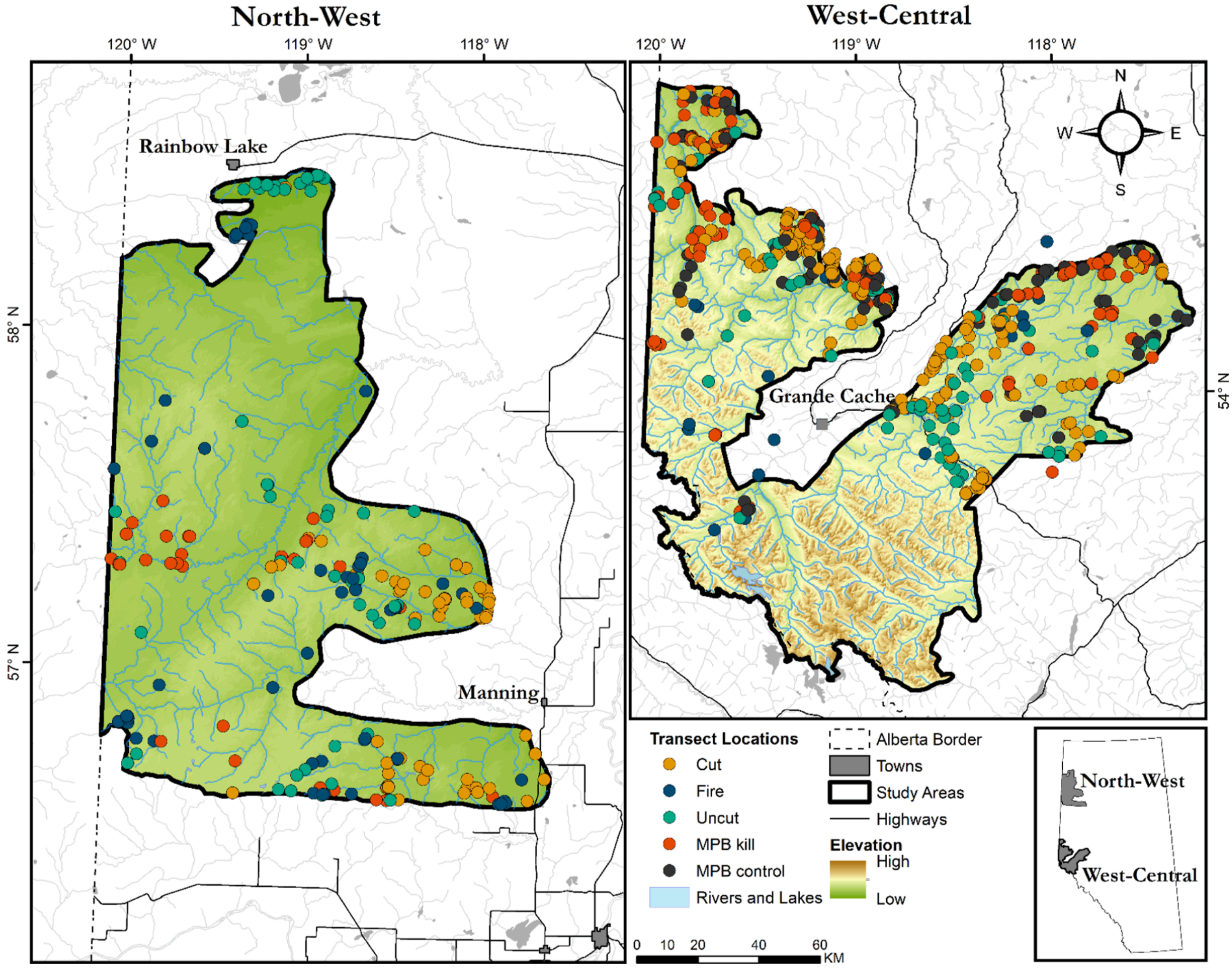

Fig. 1. North-West and West-Central study areas located in Alberta, Canada. Study area boundaries represent caribou ranges. Vegetation transect were visited in the summers of 2014 and 2015 to determine the effect of MPB on caribou and grizzly bear plant forage.

Government of Alberta. At the time of data collection, single-tree control did not occur in the north-west. Due to the remoteness of some regions, 80% of transects were between 60 m and 1 km of roads, and the remaining transects were accessed by helicopter. In the field, if transects fell within more than one stratum (e.g., uncut into cut), or included retention within cuts, we used a random bearing to move the transect into the target strata, ensuring that the transect was located ≥ 30 m from the transition between strata to reduce edge effects.

We visually estimated percent cover to the nearest percent of 25 shrub and forb taxa within six 1 m^2 or 10 m^2 circular subplots, dependent on plant size (Larsen et al., 2019); in 1 m^2 plots 1% cover is roughly the size of a fist, and in 10 m^2 plots 1% cover is roughly the size of two sheets of standard paper. Subplots were located at 5 m intervals along the 25 m transects (Table 1), We chose 25 shrub and forb taxa known to be important as grizzly bear and caribou forage (Denryter et al., 2017; Munro et al., 2006), or thought to be competitors of grizzly bear and caribou forage. We partitioned shrub and forb taxa into five categories: i) caribou forbs/graminoids, ii) caribou shrubs, iii) grizzly bear forbs, iv) grizzly bear berries, and v) competitor shrubs and forbs (Table 1). While fireweed (*Chamerion* spp.) may be consumed by grizzly bears (Gunther et al., 2014), we considered it a competitor species in this study as it is a low-quality resource with little evidence of consumption in Alberta (Munro et al., 2006), and has the ability to out-compete higher-quality resources (Delong, 1991; Landhausser & Lieffers, 1994; Pinno et al., 2014). At the centre of each subplot we visually estimated canopy cover using densiometers, and determined whether single-tree control had occurred. We then used the nearest 3 trees to the subplot centre (>5 cm diameter at breast height) to record whether MPB infestation or kill had occurred (trees with pitch tubes and/or red or grey needles), as well as percent of pine trees with MPB (MPB percent) based on a percent of all recorded trees along the transect (Table 2). Detailed field methods are described in Nobert et al. (2020).

2.3. Environmental variables

For each transect we used geographic information systems (GIS) (ArcGIS version 10.3.1 and R Statistical software version 4.0.4) to extract environmental variables. We calculated solar radiation and compound topographic index (CTI; a metric of terrain wetness where higher values depict wetter areas) from the Canadian Digital Elevation Model (Natural Resources Canada, 2015). We calculated red age, a measure of time since MPB infestation began, from the nearest red attack survey point (mean distance = 116 m, standard deviation = 512 m) conducted by the Government of Alberta, with annual surveys beginning in 2006 in both west- central and north-west study areas. We derived canopy height and canopy cover within the west-central study area from LIDAR data (Nijland et al., 2014). As LIDAR data were not available within the north-west study area, for that area we used the previously described densiometer measurements of canopy cover. For forest age (age of undisturbed forest > 50 years), and cut age (years since harvest),

Table 1
Understory shrubs and forbs recorded in plots in MPB kill or single-tree control (MPB), burned forest (fire), harvested forest (cut), or uncut/undisturbed forest (uncut) in west-central and north-western Alberta between 2014 and 2015. Shrubs and forbs were divided into groups based on their status as caribou forage, grizzly bear forage, or competitor plant taxa not known to be consumed by either caribou or grizzly bears.

Taxa	Scientific name	Plot Size
Caribou shrubs		
Alders	*Alnus* spp.	10 m^2
Birches	*Betula* spp.	10 m^2
Willows	*Salix* spp.	10 m^2
Caribou forbs/graminoids		
Creamy peavine	*Lathyrus ochroleucus*	1 m^2
Twisted stalk	*Streptopus amplexifolius*	10 m^2
Grasses	–	1 m^2
Sedges	*Carex* spp.	1 m^2
Grizzly bear forbs		
Horsetails	*Equisetum* spp.	1 m^2
Clovers	*Trifolium* spp.	1 m^2
Cow parsnip	*Heracleum lanatum*	10 m^2
Dandelion	*Taraxacum officinale*	1 m^2
Grizzly bear berries		
Huckleberry	*Vaccinium membranaceum*	1 m^2
Bog cranberry	*Vaccinium vitis-idaea*	1 m^2
Velvet-leafed blueberry	*Vaccinium myrtiloides*	1 m^2
Buffaloberry	*Shepherdia canadensis*	10 m^2
Bearberry	*Arctostaphylos uva-ursi*	1 m^2
Crowberry	*Empetrum nigrum*	1 m^2
Honeysuckles	*Lonicera* spp.	10 m^2
Lowbush cranberry	*Viburnum edule*	10 m^2
Currants	*Ribes* spp.	10 m^2
Raspberry	*Rubus idaeus*	10 m^2
Sarsaparilla	*Aralia nuducaulis*	1 m^2
Competitors		
Labrador tea	*Rhododendron groenlandicum*	1 m^2
Fireweeds	*Chamerion* spp.	10 m^2
Silvery lupine	*Lupinus argenteus*	10 m^2

Table 2
Explanatory variables used to determine abundance of understory shrubs and forbs/graminoids in four strata: MPB, fire, cut, and uncut in west-central and north-western Alberta, Canada, between 2014 and 2015. Variables are separated into related categories, where the “All” category refers to variables used in all strata models. Type describes the variable type (binary categorical, or continuous).

Strata	Variable	Type	Description
All	Combined Strata	Categorical	Combination of MPB, fire, cut and uncut strata compared to uncut[1]
	NSR	Categorical	Natural subregion class – west central: lower foothills[1], upper foothills, subalpine; north-west: lower boreal highlands[1], upper boreal highlands
	Moisture	Categorical	Measure of soil moisture based on ecosite data – mesic[1], hydric, hygric
	Nutrients	Categorical	Measure of soil nutrients based on ecosite data – poor, medium[1], rich
MPB	MPBBin	Binary	Whether MPB kill or control is present (1) or absent (0)
	MPB Percent	Continuous	Trees in plot with MPB infestation (%)
	Red Age	Continuous	Time since MPB infestation occurred (years)
	MPB Kill	Binary	Presence (1) or absence (0) of MPB killed trees
	MPB Control	Binary	Presence (1) or absence (0) of single-tree MPB control
Fire	FireBin	Binary	Whether burnt forest is present (1) or absent (0)
	CTI	Continuous	Compound topographic Index, a measure for soil wetness (index)
	Fire Age	Categorical	Time since fire event occurred grouped into 5-year intervals (years)
	Solar Radiation	Continuous	Sunlight based on slope and aspect (watt/m^2)
	Hectares Burnt	Continuous	Area burnt in a fire as a measure of fire severity (hectares)
Cut	CutBin	Binary	Whether a cut forest is present (1) or absent (0)
	Distance to Edge	Continuous	Distance to forest edge (meters)
	Planted	Binary	Whether a harvest block was replanted (1) or not (0)
	Herbicide	Binary	Whether herbicide was used (1) or not (0)
	Cutblock Age	Categorical	Time since cut event occurred (5-year intervals)
Uncut	UncutBin	Binary	Whether undisturbed forest (>50 years) is present (1) or absent (0)
	Forest Age	Categorical	Forest age (20-year intervals)
	Canopy cover	Continuous	Canopy cover (%)
	Canopy height	Continuous	Canopy height (meters)

[1] reference category.

along with block treatment data (whether a block was planted and whether herbicide was used), we used forest harvest data provided by local forest companies (Weyerhaeuser, Canadian Forest Products, ANC Timber Ltd., West Fraser Co. Ltd., Mercer Peace River Pulp Ltd.). For fire age (age since wildfire occurrence), and burned hectares (a metric for fire severity; Llorens et al., 2021), we used fire data acquired from the Government of Alberta. We derived moisture and soil nutrient classes from ecosite data made available by forest companies and the provincial government (Alberta Agriculture and Forestry, 2020). Details of environmental variables are in Table 2.

2.4. Modelling

We used zero-inflated beta regression models (glmmTMB package; Brooks et al., 2017) to model differences in understory shrub and forb occurrence and abundance among four strata (MPB [MPB kill and control combined], fire, cut, and uncut). We combined MPB kill and control strata because of the lack of observations for control in the north-west study area. We built separate models for each study area, and in each area we only modelled taxa with $\geq$ 50 observations; in west-central, this included all 25 taxa, and in the north-west this included 13 taxa (Table 1). We performed modelling in two phases, in the first phase we identified which species were affected by MPB and MPB treatments [initial models] and in the second phase we built species-specific models for those species that were identified in the first phase [final models].

First, we built 24 candidate models for all taxa in each study area to identify taxa where abundance differed among strata. Candidate models included variables describing strata (binary or combined, where uncut was the reference category), natural subregion, moisture, and nutrient regimes (Table 3). We used Akaike Information Criterion (AIC; weights (ω_i) to select the most parsimonious model for each taxa (Burnham & Anderson, 2004); carrying out AIC model selection on the abundance (mu) and occurrence (zero-inflated) portions of the model in turn, while holding the other portion of the model at the null. We combined the most parsimonious abundance and occurrence portions of the models into an initial model for each taxa (Finnegan et al., 2018).

Second, we added variables specific to each stratum to initial models (Table 2). For MPB strata (kill and control), variables included the percent of trees within the plot with MPB infestation (MPB percent), age of the MPB infestation (Red Age), a binary variable indicating whether mountain pine beetle kill was present (MPB kill), and a binary variable determining whether single-tree control was used (MPB control) (Nobert et al., 2020). For fire, variables includes an index of soil wetness (CTI; (Moore et al., 1991), fire age (grouped into 5 year intervals), solar radiation, and burn area (as a metric of fire severity). For cut, variables included distance to edge of forest (edge), herbicide use (herbicide) whether the harvest block was replanted (planted), and harvest block age (grouped into 5-year intervals). For uncut, variables included forest age (grouped into 20-year intervals), canopy cover, and canopy height

Table 3
Initial models used to determine differences in abundance of understory vegetation taxa among four strata (MPB, fire, cut and, uncut) in west-central and north-western Alberta, Canada, between 2014 and 2015. Taxa refers to individual plant species (see Table 2). We also included a random intercept to account for variation in PlotID. Variables are described in Table 2.

Model name	Model structure
null	Taxa ~ (1|PlotID)
nu1	Taxa ~ Nutrients + (1|PlotID)
ms1	Taxa ~ Moisture + (1|PlotID)
nsr1	Taxa ~ NSR + (1|PlotID)
gs1	Taxa ~ Combined Strata + (1|PlotID)
gs2	Taxa ~ Combined Strata + Nutrients + (1|PlotID)
gs3	Taxa ~ Combined Strata + Moisture + (1|PlotID)
gs4	Taxa ~ Combined Strata + NSR + (1|PlotID)
cu1	Taxa ~ CutBin + (1|PlotID)
cu2	Taxa ~ CutBin + Nutrients + (1|PlotID)
cu3	Taxa ~ CutBin + Moisture + (1|PlotID)
cu4	Taxa ~ CutBin + NSR + (1|PlotID)
fi1	Taxa ~ FireBin + (1|PlotID)
fi2	Taxa ~ FireBin + Nutrients + (1|PlotID)
fi3	Taxa ~ FireBin + Moisture + (1|PlotID)
fi4	Taxa ~ FireBin + NSR + (1|PlotID)
un1	Taxa ~ UncutBin+ (1|PlotID)
un2	Taxa ~ UncutBin + Nutrients + (1|PlotID)
un3	Taxa ~ UncutBin + Moisture + (1|PlotID)
un4	Taxa ~ UncutBin + NSR + (1|PlotID)
mp1	Taxa ~ MPBBin + (1|PlotID)
mp2	Taxa ~ MPBBin + Nutrients + (1|PlotID)
mp3	Taxa ~ MPBBin + Moisture + (1|PlotID)
mp4	Taxa ~ MPBBin + NSR + (1|PlotID)

(west-central only). For taxa that differed in abundance across multiple strata we included variables from all relevant strata. As before, we fit each side of the zero-inflated model separately while holding the other side of the equation at the null, we identified the most parsimonious model based on the lowest AIC values (we did not use weights in this portion of model selection due to the complexity and variety of models), and we combined the most parsimonious models predicting occurrence and abundance into a final model.

For the final model for each taxa, we calculated odds ratios for abundance and absence (inverse of occurrence), and the predicted relative probability of abundance and occurrence (inverse of the relative probability of absence) for significant (p-value < 0.05) categorical and continuous variables respectively. Odds ratios > 1 indicated high abundance or occurrence, and odd ratios < 1 indicated low abundance or occurrence. We validated final models using mean absolute error (MAE) and root mean square error (RMSE) calculated from model residuals. Lower values of MAE and RMSE indicate models with better predictive ability (Nobert et al., 2020) (see Appendix A).

3. Results

Although we modelled abundance and occurrence, abundance implies occurrence and may be more ecologically important than occurrence, therefore for simplicity here we focus on abundance. Occurrence results are in Appendix A. In west-central, abundance of 13 of the 25 taxa differed among strata, while in the north-west, abundance of 5 of the 13 taxa differed among strata (Fig. 2). Significant variables from final models are in Table 4. Results of initial and final model selection and complete model coefficients are in Appendix A.

In west-central, for caribou shrubs, the final alder model indicated that abundance was lower in cut and MPB control when compared to uncut and was higher in the subalpine when compared to the lower foothills. The final birch model indicated that abundance was higher in fire when compared to other strata and was higher in wetter areas (Fig. 3a). For caribou forbs/graminoids, the final grass model indicated that abundance was lower in uncut when compared to other strata, was lower in cut forest between 36 and 40 years old when compared to forests with no cut age and was higher in cut forests between 11 and 15 years old when compared to forests with no cut age.

In the north-west, for caribou shrubs and forbs/graminoids, the final alder model indicated that abundance was lower in cut when compared to other strata, was higher in the upper boreal highlands when compared to the lower boreal highlands, was higher in uncut forest between 51 and 70 years old when compared to cut and burned forests and increased with increasing MPB percent and canopy cover (Fig. 3b and 3c). The final grass model indicated that abundance was higher in cut when compared to other strata and was higher within cut forest aged between 11 and 15 years old when compared to forests with no cut age.

In west-central, for grizzly bear forbs, the final horsetails model indicated that abundance was lower in fire when compared to uncut and increased with increasing red attack age (Fig. 3d). For grizzly bear berry shrub species, the final huckleberry model indicated that abundance was lower in cut when compared to other strata, decreased with increasing MPB percent (Fig. 3b), decreased with increasing canopy cover (Fig. 3c), and was higher in the subalpine and upper foothills when compared to the lower foothills. The final velvet-leafed blueberry model indicated that abundance was higher in fire when compared to uncut. The final bog cranberry model indicated that abundance was lower in cut when compared to other strata and was higher in hygric moisture ecosites when compared to mesic moisture ecosites. The final crowberry model indicated that abundance was higher in fire when compared to other strata. The final honeysuckle model indicated that abundance was higher in stands with MPB and was higher in rich nutrient ecosites when compared to medium nutrient ecosites. The final currants model indicated that abundance was higher in fire when compared to uncut. The final sarsaparilla model indicated that abundance was higher in rich ecosites compared to medium ecosites.

In the north-west, for grizzly bear berries, the final bog cranberry and currant models indicated that abundance was higher in MPB and fire strata when compared to uncut forests. In the north-west, for competitors, the final fireweed model indicated that abundance was higher in cut when compared to other strata. In west-central, for competitors, the final fireweed model indicated that abundance was lower in uncut when compared to other strata. Fireweed abundance was also higher in the presence of herbicide application and increased with increasing MPB percent (Fig. 3b).

4. Discussion

We assessed the effects of MPB attack and MPB treatments on the abundance of shrub, forb, and graminoid forage important to caribou and grizzly bears. Generally, we found that the abundance of understory shrubs, forbs/graminoids were higher in MPB (MPB kill and control) and fire strata, than in cut and uncut strata, and this pattern was largely consistent between the two study areas. Our study builds on previous work focused on terrestrial lichens (Nobert et al., 2020) and understory shrubs and forbs (Edwards et al., 2015; Pec et al., 2015), by providing the first information on the effect of MPB and MPB treatments on understory forage important to threatened species.

4.1. Caribou shrubs and forbs

For caribou, we predicted that more intensive management treatments (cut and fire) would have generally positive impacts on shade-intolerant taxa, while less intensive treatments (MPB and MPB control) would have generally positive impacts on shade-tolerant taxa (Humbert et al., 2007). However, contrary to our predictions, we found that both intensive and less-intensive treatments affected alders, which is a typically shade-intolerant taxa (Humbert et al., 2007). Specifically, we found that in the north-west, alder abundance increased with the percent of MPB, but in west-central, alder was lower in cut and MPB control. This result suggests that MPB treatments, regardless of intensity, are likely to have a negative impact on alder abundance. In support of

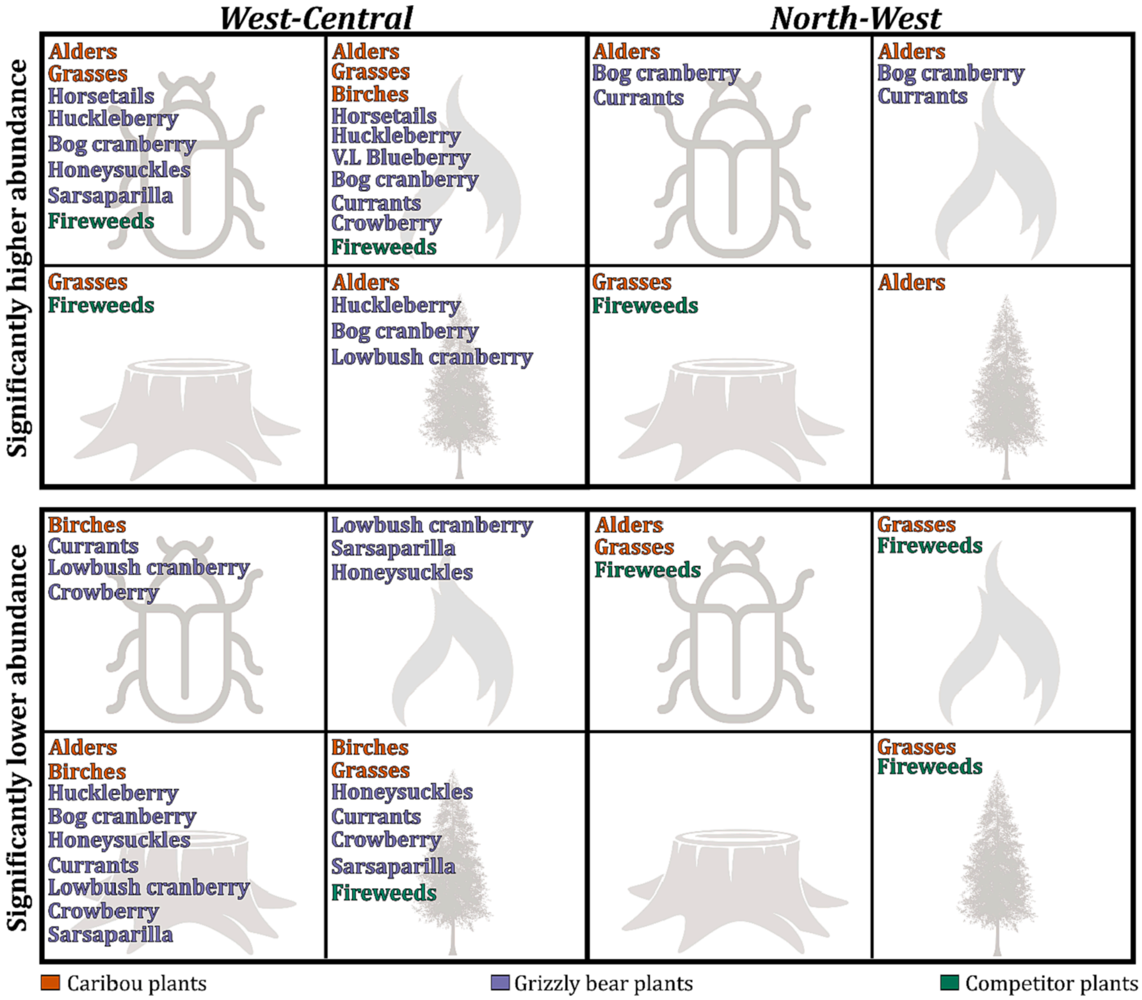

Fig. 2. Abundance of caribou and, grizzly bear plant food species, and a competitor plant that were affected by mountain pine beetle (represented by the beetle symbol), fire (represented by the flame symbol), cut (represented by the tree stump symbol), uncut (represented by the tree symbol) as determined in our first modelling stage. The top two quadrants indicate that abundance was significantly higher compared to other strata and the bottom two quadrants abundance was significantly lower compared to other strata. The two left quadrants represent the west central region, and the right quadrants represent the north-west region of Alberta, Canada.

our prediction we found that birch, which is shade-intolerant (Humbert et al., 2007) and a pioneer taxa, had a higher abundance in previously burned areas. Birch is a pioneer taxa after fire, explaining the positive impact of fire on birch abundance (Hynynen et al., 2010). Alder and birch are important caribou foods during summer and fall (Denryter et al., 2017), and our results suggest that leaving MPB kill or using prescribed burns to manage MPB may have positive impacts by potentially increasing caribou forage.

Corroborating previous research and our predictions, we found that grass, a shade-intolerant taxa, had a higher abundance in harvest blocks when compared to uncut forest (Fisher & Wilkinson, 2005; Fornwalt et al., 2018; Sekororoane & Dilworth, 1995). Specifically we found higher grass abundance in harvest blocks between 11 and 15 years old, which is in agreement with studies reporting lower abundance of forbs and grasses in newly harvested stands, with grass abundance increasing over time (Hart & Chen, 2006; Larsen, 2012; Mumma et al., 2021). Although caribou forage for grass during summer (Denryter et al., 2017), caribou generally avoid harvest blocks (DeCesare et al., 2012; Peters et al., 2013; Smith et al., 2000). This avoidance is attributed to caribou largely avoiding human disturbance (DeCesare et al., 2012; Dyer et al., 2002; Johnson et al., 2015), because harvest blocks increase caribou exposure to predation risk (Hervieux et al., 2013; Latham et al., 2011; Serrouya et al., 2011), and because caribou require large areas of intact mature forest for lichen food resources (Johnson et al., 2000; Thomas et al., 1996b; Thompson et al., 2014). Early seral habitat created by harvesting also benefits other ungulates like deer, moose, and elk, which contribute to caribou declines via apparent competition by increasing populations of shared predators in caribou population ranges (Hervieux et al., 2013; McKay & Finnegan, 2022; Serrouya et al., 2011). Therefore, although harvesting may offer fine-scale, short-term increases in caribou forage, because this forage also benefits the apparent competitors of caribou, and because harvesting increases caribou exposure to predation risk, the costs of harvesting to caribou are likely to outweigh the benefits (Nobert et al., 2020). It is possible that adaptive silviculture practices like thinning (Nadeau Fortin et al., 2016; Vitt et al., 2019), or variable retention harvesting (Franklin et al., 2019a), might balance the needs of caribou and forest sector in the face of MPB spread, but further research is needed on the impacts of these practices on caribou, apparent competitors, and shared predators.

4.2. *Grizzly bear shrubs and forbs*

Many forage species preferred by grizzly bears are shade-intolerant and/or grow in disturbed open areas, or along forest edges (Kearney et al., 2019; Lamb et al., 2017; Larsen et al., 2019; Nielsen et al., 2004b), therefore, we predicted that more intensive treatments (cut and fire)

Table 4

Odds ratios, lower (2.50%) and upper (97.50%) confidence intervals, and p-values from significant variables in zero-inflated beta regression models assessing the effect of MPB and MPB treatments on the abundance of understory taxa in west-central and north-western Alberta, Canada, between 2014 and 2015 Odds ratios above 1 indicates significantly higher abundance whereas odds ratios below 1 indicate significantly lower abundance. Complete models and results of model selection are in Appendix A. Odds ratios continuous variables are denoted with *. Variables are described in Table 2.

Taxa	Variable	Odds Ratio	2.50%	97.50%	P-value
West-Central					
Caribou shrubs					
Alders	CutBin	**0.766**	0.631	0.931	0.01
	Sub-Alpine	**1.462**	1.045	2.046	0.03
	MPB Control	**0.755**	0.592	0.962	0.02
Birches	FireBin	**3.112**	1.691	5.727	< 0.01
	CTI*	**1.305**	1.085	1.570	< 0.01
Caribou forbs					
Grasses	UncutBin	**0.768**	0.662	0.892	< 0.01
	Cut Age Class 11-15y	**1.466**	1.103	1.949	0.01
	Cut Age Class 36-40y	**0.594**	0.442	0.800	0.04
Grizzly bear forbs					
Horsetails	Combined Fire	**3.608**	1.905	6.832	0.00
	Red Age*	**1.072**	1.001	1.148	0.05
Grizzly bear berries					
Huckleberry	CutBin	**0.636**	0.509	0.793	< 0.01
	Sub-Alpine	**1.628**	1.147	2.311	0.01
	Upper Foothills	**1.454**	1.052	2.009	0.02
	MPB Percent*	**0.995**	0.992	0.999	0.01
	Canopy Cover*	**0.996**	0.993	1.000	0.03
V.L Blueberry	Combined Fire	**3.397**	1.966	5.870	<0.01
Bog Cranberry	CutBin	**0.834**	0.729	0.954	0.01
	Hygric	**1.867**	1.342	2.596	< 0.01
Honey Suckle	MPBBin	**1.248**	1.046	1.489	0.01
	Rich Nutrients	**1.349**	1.040	1.751	0.02
Currants	Combined Fire	**3.252**	1.770	5.973	< 0.01
Low-bush Cranberry	no significant variables				
Crowberry	FireBin	**1.720**	1.039	2.849	0.03
Sarsaparilla	Rich Nutrients	**2.227**	1.277	3.884	< 0.01
Competitors					
Fireweeds	UncutBin	**0.720**	0.627	0.826	< 0.01
	MPB Percent*	**1.002**	1.000	1.004	0.03
	Herbicide	**1.122**	1.017	1.237	0.03
North-West					
Caribou shrubs					
Alders	CutBin	**0.639**	0.959	0.426	0.03
	Upper Boreal	**1.698**	2.681	1.076	0.02
	MPB Percent*	**1.007**	1.012	1.002	0.01
	Forest Age class 51–70	**2.216**	4.500	1.091	0.03
	Canopy Cover*	**1.006**	1.011	1.001	0.02
Caribou forbs					
Grasses	CutBin	**2.086**	3.629	1.199	0.01
	Cut Age Class 11-15y	**3.532**	8.365	1.491	< 0.01
Grizzly bear berries					
Bog Cranberry	Combined Fire	**1.732**	2.454	1.223	< 0.01
	Combined MPB	**2.254**	3.630	1.400	< 0.01
Currants	Combined Fire	**1.469**	2.164	0.997	0.05
	Combined MPB	**2.760**	5.299	1.438	< 0.01
Competitors					
Fireweeds	CutBin	**1.480**	1.854	1.181	< 0.01

would have a positive effect on the abundance of grizzly bear foods, which are generally shade-intolerant or disturbance-tolerant taxa (Colton et al., 2021). In support of this prediction, we found that fire did have a positive impact on abundance of grizzly bear foods. Specifically, horsetails, velvet-leafed blueberries, currants and crowberries in the west-central study area, and bog cranberry and currants in the north-west study area, all increased in abundance in burned areas. However, contrary to this prediction, we found that grizzly bear plant-food abundance did not increase in harvested areas, and that harvesting decreased the abundance of huckleberry and bog cranberry in the west central study area. As fire suppression efforts continue in grizzly bear habitat, harvest blocks are used extensively by grizzly bears as a surrogate of wildfires (Nielsen et al., 2004a; Souliere et al., 2020). Differing response of forage species to fire and cut provides further evidence that these two disturbances affect succession differently (Franklin et al., 2019b; Hart and Chen, 2008). Successional differences are likely driven by differing soil disturbance during harvesting as well as post-harvest silvicultural treatments (mechanical site preparation, herbicide) in areas of the same age (Franklin et al., 2019b; Hart & Chen, 2008; Nguyen-Xuan et al., 2000). Although we included silviculture data in our models, we only included herbicide application and these data were potentially too coarse to link to abundance of individual taxa. Evaluating the differences between fires and harvested areas, and how these are impacted by silvicultural practices, will provide more insights into the impacts of different MPB treatments on grizzly bear foods, and will provide information to guide ecosystem-based management within grizzly bear population ranges.

For less intensive MPB kill and control strata, we predicted less of an impact on grizzly bear plant food abundance. In accordance with this prediction, we found the MPB strata affected fewer grizzly bear plant-food species than more intensive treatments. We found that in the west-central study area, older MPB infestations were associated with increased abundance of horsetails and, while MPB was associated with an increased abundance of honeysuckle, huckleberry abundance decreased with increased MPB percent. In the north-west study area, MPB was associated with increased abundance of bog cranberry and currants. Overall, these results suggest that huckleberry abundance increases in undisturbed forest and in open- to moderate- canopy cover, and that honeysuckle, currants and bog cranberry respond positively to less intensive disturbance like MPB that partially opens the canopy (Nielsen, Munro, et al., 2004; Smreciu et al., 2013). Huckleberry constitutes one of the largest portions of grizzly bears diets in fall (Munro et al., 2006) and provides grizzly bear with calories important in sustaining hibernation throughout the winter (Pigeon et al., 2016). While we found that huckleberry abundance decreased with increased MPB, we also found that abundance was highest in more open canopies. It is possible that forest harvest practices that partially open the canopy, for example selective thinning to remove mountain pine beetle affected trees, or to remove trees susceptible to MPB infestation, may have positive impacts on grizzly bear foods like huckleberry, currants, honey suckle, and bog cranberry by opening canopies and reducing competition (Pec et al., 2015).

4.3. *Competitor shrubs and forbs*

While fireweed may be consumed by grizzly bears, we considered it a competitor species as it occurs in disturbed areas and may suppress higher quality wildlife forage (Landhausser & Lieffers, 1994; Pinno et al., 2014). We found that fireweed abundance was higher in cut forest. In west-central, fireweed abundance was also higher in harvest blocks where herbicides had been applied. Our results suggest that fireweed is positively impacted by disturbance and that the application of herbicides may increase fireweed abundance (Strong & Gates, 2006), potentially allowing fireweed to outcompete and decrease the abundance of other important wildlife forage (Delong, 1991; Landhausser & Lieffers, 1994; Pinno et al., 2014). Furthermore, fireweed is an important component of elk, mule deer, and moose diets (Strong & Gates, 2006), and may have negative effects on caribou through apparent competition, and increased predator risk (Hervieux et al., 2013; Serrouya et al., 2011; Sorensen et al., 2008).

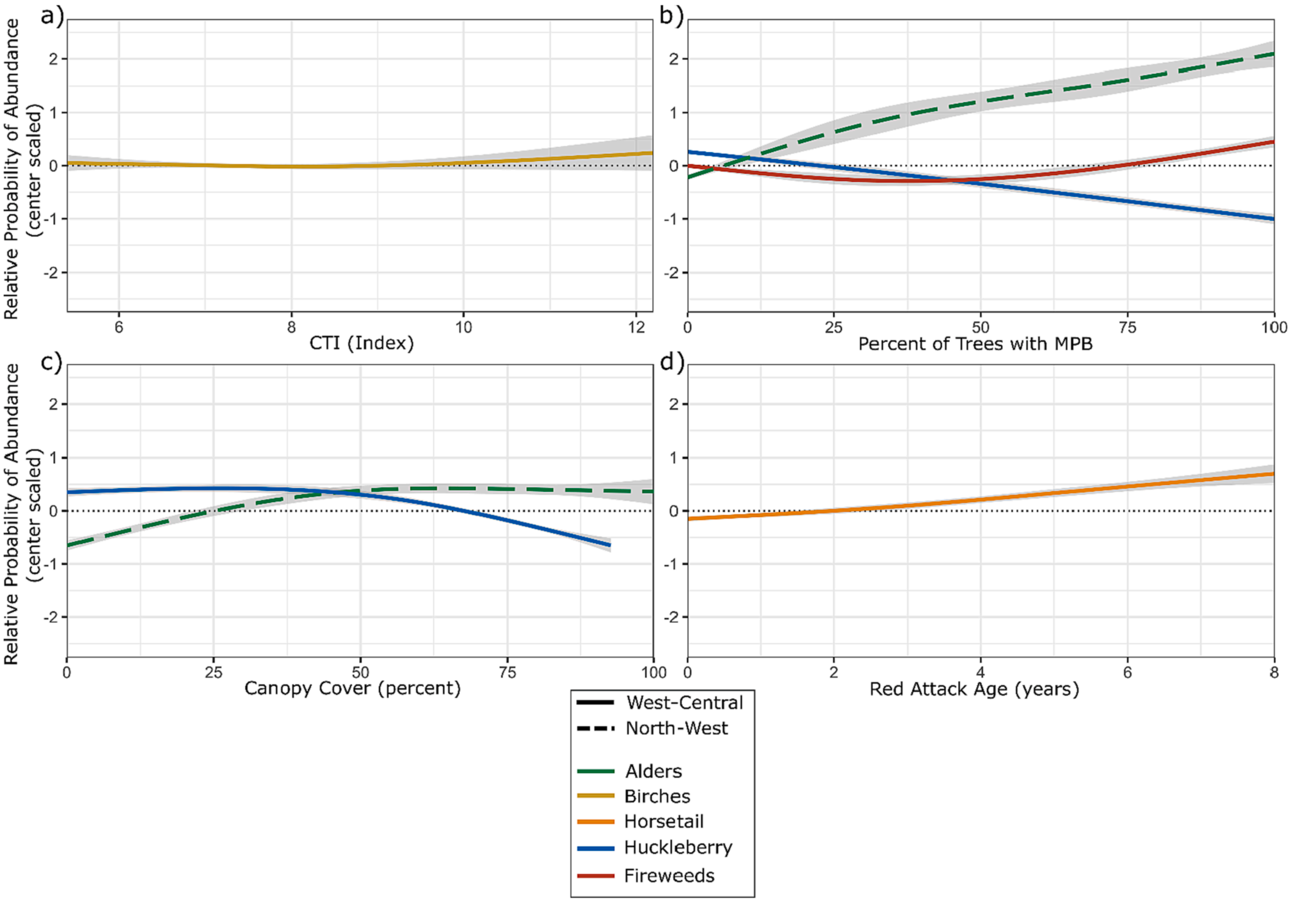

Fig. 3. Relative probability of abundance from zero-inflated beta regression models assessing effect of variables related to MPB and MPB management in west-central and north-western Alberta, Canada, between 2014 and 2015. Taxa in west-central are denoted with solid lines, and taxa in the north-west are denoted by dashed lines. Shaded areas indicate 95% confidence intervals.

4.4. Limitations

First, we had an uneven sample size within our two study areas, which made comparison between the two areas difficult. Also, single-tree cut and burn MPB control did not occur within the north-west study area, which limited our data set and prevented us from comparing how the impacts of single-tree cut and burn differed across study areas. Second, because MPB infestations in Alberta were relatively recent (~2006), at the time of data collection, we were unable to assess the impacts of MPB beyond 8 years, while we sampled harvest blocks and fires up to 40 years after disturbance. Third, our study did not account for fire intensity or mechanical silviculture treatments, such as scarification, which has impacts on canopy removal and understory taxa growth (Fornwalt et al., 2018; Nielsen et al., 2004b). Future research should include data collection in areas that have been impacted by MPB over longer timeframes (>8years), and should consider the impacts of fire intensity and silviculture treatments. This could provide additional insights into the impacts of MPB and MPB management on important forage taxa for threatened species.

4.5. Management implications

Generally, we found that many taxa had positive responses to MPB and/or fire, possibly indicating adaptation to these natural disturbances. These findings are corroborated by research from British Columbia, Canada, which found that the initial canopy opening associated with MPB kill, and low- to moderately high-severity burns, resulted in a converging understory community (Edwards et al., 2015), possibly due to reduced canopy cover and increased availability of nutrients after tree death (Pec et al., 2015). Our results suggest that less intensive MPB control and prescribed fires might be effective management options which balance the threat of MPB against maintaining food resources for threatened species. It also is possible that canopy thinning and variable retention harvesting, which aim to mimic natural canopy openings, mitigate effects of harvesting on biodiversity in mature forests, and may maintain caribou habitat (Franklin et al., 2019a; Nadeau Fortin et al., 2016), and terrestrial lichens (Vitt et al., 2019), may be a viable solution to address the needs of forest sector and threatened wildlife species in the face of MPB spread, however further research is needed on the impact of canopy thinning and, variable retention harvesting on multiple wildlife species.

4.6. Conclusion

Balancing recovery actions for threatened species against threats to resource extraction activities is complex (Pimentel et al., 2005). By providing information on the impacts of MPB and MPB management on important forage for threatened species, our study has provided information that could be used for science-based management where caribou, grizzly bears, and MPB co-occur. In accordance with Pec et al. (2015) we confirmed that MPB and MPB management impact understory vegetation preferred by wildlife, and like Nobert et al. (2020), our results suggest that less intensive MPB treatments may provide a balanced management option for multiple boreal forest values.

As MPB continues to be a significant problem in Alberta, and potentially across the boreal forest (Cooke & Carroll, 2017; Shegelski et al., 2021), the results from our study, combined with ongoing assessments on the impact of MPB on movement and habitat use of other wildlife species provides essential information for evidence-based landscape management (Carwardine et al., 2019; Lundquist et al., 2002). For example, to address a large-scale infestation prescribed burns may be the most effective way to eliminate the threat while maintaining caribou and grizzly bear forage, while at finer scales single-tree control provides a balance between maintaining forage for threatened species and mitigating the impacts of MBP infestations on forestry. The merit of studies like ours which consider multiple species and values is increasingly recognized (e.g. Finnegan et al., 2021; Franklin et al., 2019a,). This approach allows decision making to draw upon a larger breadth of information (Lundquist et al., 2002), and enables managers to weigh the benefits and costs of decisions for multiple species (Carwardine et al., 2019; Martin et al., 2012).

CRediT author statement

Cameron McClelland: Methodology, Software, Validation, Formal Analysis, Investigation, Data Curation, Writing - Original Draft/Review and Editing, Visualization. **Barry Nobert:** Methodology, Investigation, Data Curation, Writing - Review and Editing. **Terrence Larsen:** Conceptualization, Methodology, Investigation, Writing - Review and Editing, Supervision, Funding Aquisition. **Karine Pigeon:** Methodology, Investigation, Writing - Review and Editing, Supervision. **Laura Finnegan:** Conceptualization, Methodology, Investigation, Resources, Writing - Review and Editing, Supervision, Project Administration, Funding Aquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.120841.

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